THE COMPARATIVE HISTOLOGY OF THE DIGESTIVE TRACT.

EDITH J. CLAYPOLE, PH. B., M. S.

The idea of the evolution of the complex from the simple has never been more prominently before the eyes of the scientific world than it is today. It has become, as it were, the underlying working hypothesis in almost every line of research, turning attention strongly toward the questions surrounding the origin of adult and highly differentiated structures from preëxisting simple types. The internal structures of animals, though useless for establishing specific or even generic differences, yet afford a basis for the establishment of certain broad *historic* relations, which indicate the path of the past development of the race. This has been long shown to be true of the gross fórm of parts, but the application of the same principle to histological variations is not so general. It is from this point of view that I wish to discuss the digestive tract, which is chosen simply because it is so well known in the higher types and more readily worked up in those concerning which literature is not so abundant. Many points are as yet incomplete and this presentation must be considered, more in the line of suggestion than as a treatise on the subject.

The forms chosen cover as wide a field as possible from the mammals to the fishes, though, personally, I could examine and section the tissues of one representative of each class, excepting in the case of the *Amphibia*. There are the *Mammalia*, from which the cat is taken ; the *Aves*, represented by the pigeon; the *Reptilia*, for which the turtle stands; the *Amphibia*, a group containing many divergent forms, can be far more easily obtained and, besides, the frog (*Rana catesbiana*), the mud puppy (*Necturus maculatus*), the mud dog (*Cryptobranchus alleghaniensis*) have been used. Of the *Pisces*, the work of Dr. Hopkins, of Cornell University, gives the structure in American Ganoids and other forms can be used readily. The Lamprey *Petromyzon* is added to the list and completes it. Many more could have been chosen had time afforded, but these must stand to show a few general points of interest.

Mammalia.—The structure of the digestive tract in this class is so familiar that it is only necessary to give the essential characters with no detailed description. Though subject to wide variation, due to differences in food, in the main the same plan of structure persists in all. Epithelium lying on a basement membrane lines the whole tube; from the lips to the stomach stratified squamous cells are present; from the stomach to anus the simple columnar cell forms the unit of structure. Certain modifications exist at definite points.

1. The respiratory part of pharynx (to soft palate) is lined with stratified columnar cells.

2. The cardiac gastric glands of the stomach have the *parietal* or acid cells, so important in aiding the rapid digestion of fibrin and albumen.

3. The small intestine has its surface thrown into villi, which are covered with striated epithelial cells, especially active in absorption.

4. All the parts of the tract are quite sharply marked off from each other (excepting the mouth and pharynx).

Aves.—The birds are the nearest existing allies of the mammals and although they represent an extreme development from a more primitive stock, have at least warm blood in common with their brother man. Almost as various forms are found here as among mammals, the variation being due to the same cause—variation in food. Both grain-eaters and meat-eaters exist in this class and since in the laboratory the pigeon is the bird most easily obtained in the proper condition for examination, it is on this form that the following facts are based :

As before, the whole tract is lined with epithelium ; from the mouth to stomach stratified squamous cells cover the surface ; the respiratory part of the pharynx shows the same difference. In the pigeon, and grain-feeders generally, the esophagus dilates into a crop, not a glandular organ, the so-called *pigeon's milk* being the cast off and disintegrating epithelial cells. The differentiation of the stomach into two organs, one glandular, the other muscular, brings in a little change in structure at this point. The proventriculus or true stomach has only a chemical function. It is set thickly with glands, which are changed from the simple tubular of the mammal to compound tubular of a complex form, a large number of small tubes opening into one common duct. In the most complex form there is almost a suggestion of chains of cells, so closely do the adjacent tubes lie against each other, only a single row of connective tissue cells lie between. The deep-lying cells are the usual polyponal secreting cells. This apparently great modification from the simple tubular glands of the mammals is merely a device for saving space and for putting a large secretive area in a small organ. Since the food is not here subjected to the grinding and mixing process, there is no reason for the part to be large, it is merely a glandular structure, in passing through which the food is bathed with a juice, powerful in chemical action. The change from the esophagus to stomach is very gradual ; above the crop the walls are entirely free from glands ; between crop and proventriculus mucous glands appear, becoming larger toward the latter part. They are compound tubular structures, the mouth being lined with low cuboidal cells, while the deep-lying secreting gland tubes are formed of the usual polyhedral cells. As shown from the light stain taken if hematorylin is used, they are mucous glands. The surface is covered with a layer of stratified squamous cells, which grows thinner as the stomach is approached. Finally, these are replaced by the simple columnar cells, characteristic of this organ. At the same time the complexity of the gland increases and the cells change from mucous to serous for the secretion of the true gastric juice.

This gradual change in the glands is very suggestive of the manner of development of the large glands in the body from their originally single tube or sac; it gives almost a bird's eye view, as it were, of the transformation, by tracing the change in these from the crop to proventriculus.

In the gizzard the surface is protected by a hardened layer, formed as a secretion from the underlying cells, which are simple columnar, as in the stomach. The function of this organ is a purely mechanical one, hence the great development of the muscle coats surrounding the hardened mucous layer. The intestine differs but slightly from that of the mammal, the muscle coats are very thin, the mucous surface, lined with simple columnar striated cells, is thickly set with villi from the gizzard to cloaca. At first tall and slender they gradually become shorter and thicker, disappearing entirely in the neighborhood of the cloaca.

The notable differences are the following:

1. Development of compound tubular glands in the lower part of the esophagus and stomach.

2. Villi reach through intestine to cloaca, usually disappearing there.

3. Loss of distinctness between certain parts, *i. e.*, esophagus and stomach, large and small intestines.

Reptiles.—But one reptile can stand here to represent the class, the Turtle. So that exception to the following facts may be taken if some other form were chosen. The turtles, however, show some interesting variations. The mouth in all forms is lined with stratified squamous epithelium, which at times is replaced by stratified columnar apparently without any definite cause. If there are many papillæ or similar structures in the mouth, according to Machate, they are liable to be covered with stratified squamous, while stratified columnar cell line the vallies between. If the mouth is horny at all, then the epithelium is always of the stratified squamous form.

In the esophagus there are two distinct structures found. All the great sea turtles (Hoffmann) have in the esophagus peculiar horny papillæ, which may extend even into the stomach. In these forms the esophagus and the papillæ, even those in the stomach, are coated with stratified squamous epithelium. In all other turtles the esophagus is lined with stratified, columnar, ciliated cells, and mucous glands are largely developed. In both cases the muscle of this part of the tract is the plain kind, as in the birds.

There is no sharp definition between the esophagus and stomach, but where the characters of the latter are well established they are seen to be not unfamiliar. The cardiac glands are simple, tubular in form, the pyloric ones being wider in mouth and less deep. Simple columnar epithelium covers the surface and there is a total lack of peptic cells. The cells do not vary much in appearance, but no doubt physical and chemical differences exist among them.

The intestine begins with a very sudden decrease in size, inside, the mucous coat is thrown into longitudinal folds. The simple columnar epithelium of the stomach is continued into this part ; among the columnar cells is a varying number of goblet cells. But there is a total absence of *villi*, so characteristic of the small intestine in both birds and mammals. Glands are present in some families of turtles and absent in others. In the one studied (*Chripenny picta*) very small tubular structures were found. The change from stomach to intestine is sudden, the pyloric glands abruptly ending, the structure of the intestine appearing. The large intestine is like the small, except that the walls are thinner. The cloaca is marked by a large amount of pigment and large mucous glands.

Several significant changes appear here:

1. Presence in some forms of ciliated columnar epithelium in esophagus as well as respiratory tract.

2. Absence of villi in all forms.

3. Excepting for the division between the stomach and small intestine and the large and small intestines all the parts are indistinctly separated from each other.

Amphibians.—In this comprehensive group we reach the parting of the ways. To even more generalised forms than these, we must look in past ages to see the origin of the higher types. Some few of the old-fashioned forms no doubt, with small changes in fashion, have lived on and are now included among this group. Hence our interest in them is great.

They show extremes of type, as in the frog and toad on one hand and the simple, primitive (sub-salamander) *Necturus* on the other. The gross structure of the first form is somewhat similar to that of the turtle—a large, wide mouth and esophagus, merging gradually into the narrow stomach, this somewhat sharply passes into the small intestine, which also is fairly distinct from the short, broad, large intestine. In *Necturus*, the other extreme, the short, wide esophagus passes insensibly into a stomach not very much larger; this, in turn passes quite gradually into the small intestine. There is no large intestine, the small one opening into a wide cloaca.

Summarising these forms as well as possible, we find the following points of structure:

There are two types of mouth lining and esophagus:

1. All purely aquatic *Amphibians* have, according to Kingsbury, stratified squamous epithelium. A layer of but four to five cells, however, in the mouth; in the esophagus these are replaced by simple columnar ciliated cells.

2. All the remaining land and semi-land forms have the roof of the mouth and the esophagus covered with stratified ciliated cells, while the tongue and floor of the mouth are protected by stratified squamous epithelium.

A gradual transition from esophagus to stomach brings us to the usual structure, simple columnar cells and the characteristic tubular glands. The change from simple columnar ciliated to the non-ciliated form in the purely aquatic *Amphibians* makes but a slight difference between these organs. There are no acid cells in *Necturus* and its allies, and it is yet an open question whether they exist in the frog.

The small intestine is not widely different, a tube lined with the simple columnar cells, in some forms showing tubular glands, in others not. The large intestine, if present, is practically the same, except for an increase in the number of mucous cells. The cloaca is in some forms ciliated, in others lined with stratified columnar cells. The changes to be noted here are :

1. Introduction of simple epithelium in esophagus of some forms.

2. Increased indefiniteness of gross parts (esophagus, stomach, intestine).

3. Very great increase in size of cellular elements.

There is one class yet to be mentioned, also an ancient race, that of the Ganoid fishes. From Dr. Hopkins' work on the American Ganoids we find the following points established :

As far as the pneumatic duct or opening of the air chamber into the mouth, the mucous coat consists of stratified squamous cells ; from there simple columnar ciliated cells take their place until two to three centimeters from the pyloric part of the stomach, when the cells become non-ciliated. Gastric glands are present for the first time in the class "fishes."

One word for the lamprey, as shown by Claypole. In them the whole enteron, from mouth to cloaca, is lined with simple epithelium ; no stratified layer appears at all. The esophagus shows simple columnar and the intestine ciliated areas of columnar cells intermingled with non-ciliated masses.

We have here before us the evolution of the mammalian alimentary tract. From a simple straight ciliated tube it passes through both cellular differentiation and gross differentiation, until the adult enteron, with all its complexity of parts and structures, is complete. Ciliated epithelium is primitive and in the adult mammal is present, as we have seen, only in the respiratory part of the pharynx. In birds the same is true. In turtles one group agrees with the foregoing types, while the second gives us ciliated stratified cells in the esophagus. *Amphibians* show practically the same distribution of these cells as in turtles, with an added ciliated area in the roof of the mouth in land forms. Ganoid fishes extend the area for ciliated cells to the stomach also, but omit them in the mouth, and among the *Cyclostomes* the whole intestinal tract is more or less covered with these primitive elements. But one cause can account for this almost complete banishment: the demand for rapid absorption in the quick-moving, active animals, to repair the waste of such activity makes the necessity great for surfaces covered with columnar striated cells in those parts where such processes take place, *i. e.*, stomach and intestines. The protective coat of stratified squamous cells is essential also in the smaller, longer tubes, which serve as the esophagus among birds and mammals. The development of villi in birds and mammals is another answer to the demand for absorptive area.

One even more significant point remains, that is the size of the elements in the various forms. It is a striking fact that in ascending the scale of life among animals, there is a very general loss of size in the cells of the body. The generalised *Amphibians* show us the largest cells known—*Amphiuma*, *Necturus*, *Cryptobranchus*, frogs and toads show a fair graded series in size. Among turtles they are still large, considerably smaller in birds and smallest of all among mammals. In the Plate this fact is illustrated in Figures 1-5. The cells lining the small intestines were chosen to represent this truth since of all the parts of the digestive tract this one perhaps is subject to least variation in structure and function. The cells were drawn to scale and from specimens similarly prepared. They need no further explanation.

The story is but that of the change from a colony of a few large, not highly specialised units, into one composed of very many small, but more highly specialised. By this decrease in size two important points are gained: rapid removal of formed compounds, both waste products and useful substances and rapid additions of new materials, and oxygen can be rapidly obtained from the circulating blood and in all ways far more rapid transportation is accomplished. From this point of view the practical necessity for a change of size in all the cells in the body becomes apparent. Each one gains equally in effecting complete and rapid removal of waste and the results are beneficial to the whole organism, resulting in a heightened power of adaptation to the needs of life.

REFERENCES.

1. 1890. Bronn—Klässen und Ordnungen des Thierreichs (Reptilien). Bd. VI., T. III.
2. 1891. Bronn—Klassen und Ordnungen des Thierreichs (Vögel). Bd. VI., T. IV.
3. 1894. Claypole, Agnes M.—The Enteron of the Cayuga Lake Lamprey. Proceed. Am. Mic. Soc., 1894.
4. 1893. Hopkins, G. S.—The Enteric Epithelium of *Amia calva*. Wilder Quarter Century Book, 1893.
5. 1895. Hopkins, G. S.—The Enteron of American Ganoids. Journal of Morphology, Vol. XI, No. 2.
6. 1894. Kingsbury, B. F. The Enteron of *Necturus maculatus*. Proceed. Am. Mic. Soc., 1894.

PLATE I.

Fig. 1. Vertical section of intestinal epithelium of cat, showing high columnar cells with a striated border.

Fig. 2. Vertical section of intestinal epithelium of pigeon. Same parts shown as above.

Fig 3. Vertical section of same part in turtle.

Fig. 4. Vertical section of frog's intestine.

Fig. 5. Vertical section of intestinal epithelium of *Cryptobranchus.*

All these sections are from tissues similarly prepared so as to give uniform conditions of hardening, etc. The cells show more or less distinctly the striated border characteristics of absorptive cells.

Figs. 6, 7 and 8, are vertical sections of the esophagus of the cat, turtle and pigeon, showing the stratified squamous cells in the two warm-blooded cells and the stratified ciliated columnar cells in the turtle.

PLATE I.

Fig. 1.

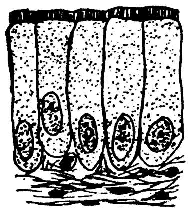


Fig. 2

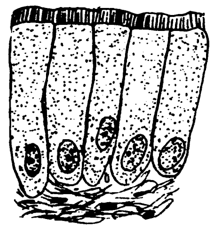


Fig. 3.

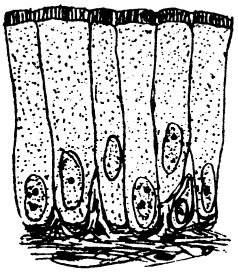


Fig. 4

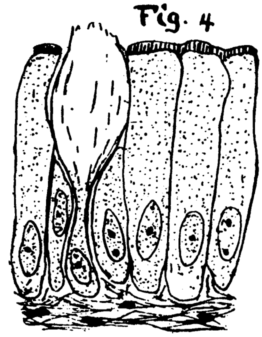


Fig. 5.

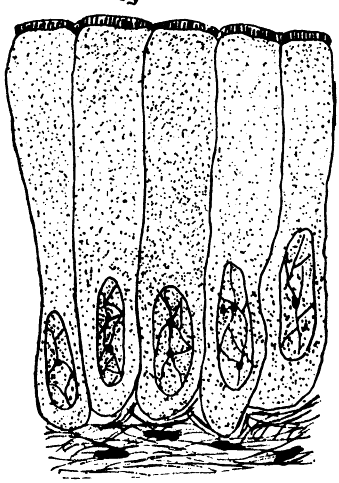


Fig. 6

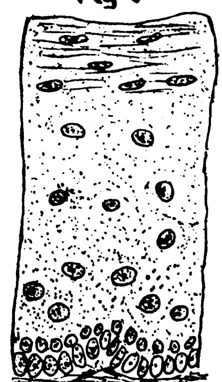
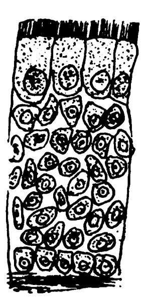


Fig. 7.



1/100 m.m.

Fig. 8.